

RHYTHM OF FECAL PRODUCTION AND PROTEIN CONTENT FOR BLACK-TAILED JACKRABBITS

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ABSTRACT.— The cyclical phenomenon of soft and hard formation of feces in desert black-tailed jackrabbits (*Lepus californicus deserticola*, Mearns) was investigated. Sixty-nine blacktails were shot between 0525 hours and 1508 hours over a 4-day period. The average age was 314 days for all black-tails. The large intestine was removed and linear measurements taken. Overall length of the large intestine averaged 163.3 cm; mean length of the colon was 51.5 cm and average length of the rectum was 111.8 cm. Moisture content for soft and hard pellets averaged 79.5 percent and 74.1 percent, respectively. Protein content of soft and hard pellets averaged 45.8 percent and 14.3 percent, respectively. The black-tails began the transition from hard to soft pellets as early as 0414 hours, and nearly all had completed the reverse transition by 1508 hours. Female black-tails began both early morning and afternoon transitions significantly later than the males. Reasons for the apparent sexual partitioning are proposed.

It has long been known that the domestic rabbit produces both hard and soft fecal pellets (Morot 1882). The hard pellets are the normal waste product of the digestive tract and are the type of feces found in the field. The soft "pellets" are a special product of the cecum, and are reingested directly from the anus and swallowed whole. The position assumed by the black-tailed jack rabbit when reingesting soft pellets is described by Lechleitner (1957).

The method whereby a rabbit can pass two kinds of feces, soft and hard pellets, has been conjectured by Eden (1940) and Thacker and Brandt (1955). The latter suggest hard fecal pellets are formed by material that has passed through the base of the cecum without being mixed with the main content of the cecum. The soft feces are formed by emptying the major portion of the cecum, in a cyclic manner, by a strong contraction of the spiral muscle (Thacker and Brandt 1955). The composition of the soft feces is comparable to that of the cecal contents in protein, crude fiber, and other proximate nutrients (Eden 1940, Olsen and Madsen 1944). Cecotomized rabbits do not excrete typical soft feces (Herndon and Hove 1955). Although the hard pellets exit the body as firm, nearly spherical excreta, the soft feces are generally excreted as clusters of soft, moist, pellets with

a distinctive sheen. Soft feces usually are higher in protein than hard feces (Herndon and Hove 1955). Soft pellets consist largely of bacteria surrounded by a proteinaceous membrane deposited posterior to the colon (Griffiths and Davies 1963).

Several authors have reported the cycle or rhythm of production of hard and soft pellets in rabbits. Although Southern (1942) reported the frequency of coprophagy (or cecaphagy) in the wild rabbit as twice daily, most authors suggest a single such daily period (Meyer 1955, Watson and Taylor 1955, Lechleitner 1957). Spencer (1955) studied rhythms of reingestion in white-tailed jackrabbits (*Lepus townsendii*), snowshoe hares (*L. americanus*), and New England cottontails (*Sylvilagus transitionalis*). Hansen and Flinders (1969) suggested that reingestion in white-tailed jackrabbits, black-tailed jackrabbits, snowshoe hares, and European hares takes place in the late morning hours. Thacker and Brandt (1955) found that the excretion of hard and soft feces by domestic Dutch rabbits was a consistent daily phenomenon both as to time and quantity. Lechleitner (1957) reported the percent of soft feces in the recta of 160 black-tailed jackrabbits killed periodically throughout every month of the year. Although the exact time of death was not known, it had been approximated for the 160

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black-tails. However, no known study reported to date has attempted to quantify the exact periodicity of soft and hard feces formation in wild populations of black-tailed jackrabbits.

The purpose of this study was to quantify the exact time periods of production as well as transition periods for hard and soft feces in wild populations of black-tailed jackrabbits in north central Utah.

STUDY AREA

This study was conducted in two areas in north central Utah. Rabbits were sampled from rangelands near Fountain Green, Sanpete County, Utah, and from the U.S. Forest Service Benmore Experimental Area near Vernon, Tooele County, Utah. The elevation of the study areas are approximately 1830 m and 1770 m, respectively. Each receives about 35 cm of average annual precipitation, with most of this in the form of snow from October through May.

The woody vegetation of both areas is dominated by rubber rabbitbrush (*Chrysothamnus nauseosus*) and big sagebrush (*Artemisia tridentata*). Prominent grasses include bluebunch wheatgrass (*Agropyron spicatum*), fairway wheatgrass (*A. cristatum*), and Sandberg bluegrass (*Poa sandbergii*).

METHODS

Desert black-tailed jackrabbits were collected with shotguns on four days during March 1980. Predawn collections were conducted with the aid of a spotlight. The first 59 black-tails were collected from the Fountain Green study area: 8 black-tails on 8 March, 19 blacktails on 15 March, and 32 blacktails on 18 March. An additional 10 black-tails were taken 22 March from the Benmore study area.

All black-tails were taken opportunistically, and the exact time of death to the nearest minute was recorded for each hare shot. An attempt was made to sample black-tails during all time periods between initiation of the hard-to-soft pellet transition in early morning to the soft-to-hard pellet transition in the early afternoon. Entrails of the black-tails were removed within 3 hours after being shot, and frozen.

The left eyeball was removed for age determination using the eye lens-weight method and age curve described by Tiemeier (1965). The eyeball was held in 10 percent buffered formalin for one week. The lens was then removed from the eyeball and placed in an oven at 90 C. The lens was considered dry after 48 or more hours, when repeated weighings to 0.001 g resulted in no additional weight loss.

In the laboratory, the portion of the intestinal tract from the anus to the juncture of the small intestine and ileocecal valve were separated by severing the mesentery. The overall length of the large intestine from the ileocecal valve to the anus was measured, as well as the length from the ileocecal valve to the taenia coli muscle. Fecal samples of both hard and soft pellets were taken, if present, from the rectum (between taenia coli muscle and anus). Hard pellets could not be accurately separated from soft pellets in the large intestine until the feces passed the taenia coli muscle. If a transitory condition between hard and soft pellets was noted, the length of the rectum between the transition and taenia coli muscle was measured. The precise time the transition occurred at the taenia coli muscle was calculated by backdating the transition for a 45 cm per hour rate of passage. Fecal samples were immediately weighed to 0.001 g, and then placed in a drying oven at 83 C for 24 hours to determine moisture content.

Within approximately one month, the fecal samples were again oven dried, cooled in a dessicator, ground, and analyzed for nitrogen content using the macro-Kjeldahl technique (Black et al. 1965). Samples of feces <1 g were pooled with fecal samples from black-tails of the same sex that were collected at approximately the same time.

RESULTS AND DISCUSSION

Measurements

The 69 (33 males, 36 females) black-tailed jackrabbits were collected between 0525 hours and 1508 hours. The average age for all black-tails was 314 ± 141 days (SD) ($N=67$, range 153–746 days). The average age for males was 315 ± 142 days ($N=31$, range

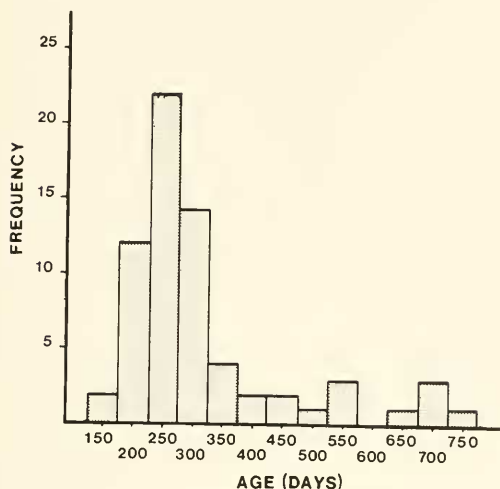


Fig. 1. Histogram illustrating age distribution in days of black-tailed jackrabbits collected for analysis.

153–718 days) and for females was 313 ± 143 days ($N=36$, range 169–746 days). The average age by 50-day intervals for black-tails in our sample is illustrated in Figure 1. Black-tails born during 1979 comprised 84 percent of the sample; all remaining black-tails were born during 1978. Seventy-two percent of all black-tails collected were between 175 and 325 days of age and were born during the period June through September. A breakdown by year and month for black-tails born in 1978 and 1979 is represented in Figure 2.

The average overall length of the large intestine was 163.2 ± 17.2 cm ($N=66$, range 134–212 cm). The mean length of the colon was 51.5 ± 5.0 cm ($N=66$, range 43–72 cm) and of the rectum was 111.7 ± 14.6 cm ($N=66$, range 85–143 cm). Correlation between the measurements of overall length of the large intestine ($r=0.31$, $P < 0.05$), colon length ($r=0.25$, $P < 0.05$), and rectal length ($r=0.29$, $P < 0.05$) with age of the black-tail was relatively low. However, correlation between the overall length of the large intestine and colon length ($r=0.62$, $P < 0.001$) and the overall length of the large intestine and rectum length ($r=0.96$, $P < 0.001$) was much higher. The correlation between colon length and rectal length was $r=0.38$ ($P < 0.005$).

Average percent moisture of soft pellets from 58 samples collected from the rectum was 79.5 ± 1.8 percent (range 74.2–83.0 percent). Average percent moisture of hard pellets from 20 samples collected from the rec-

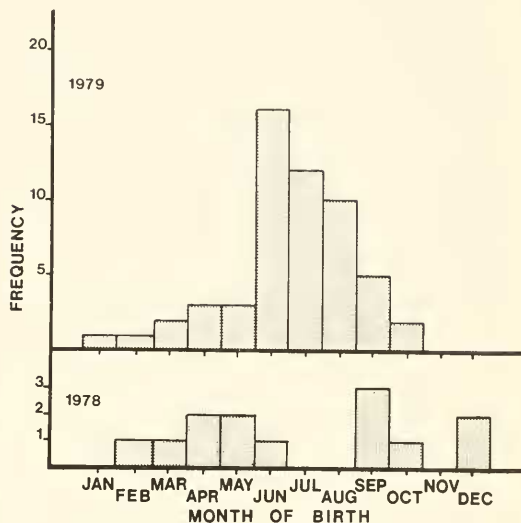


Fig. 2. Distribution of months of birth for black-tailed jackrabbits collected for analysis that were born during 1978 and 1979.

tum was 74.1 ± 2.8 percent (range 67.8–78.8 percent). The average moisture content for soft pellets was significantly greater ($P < 0.001$) than that of hard pellets using an unpaired T-test. This comparison included 12 samples where hard and soft pellets were removed from the same rectum. This indicates a significant change in moisture content associated with the rapid change in the type of pellet produced at the taenia coli muscle.

Protein

Protein content (percent $N \times 6.25$) of soft and hard pellets averaged 45.8 ± 5.9 percent ($N=8$, range 35.0–51.5 percent) and 14.3 ± 5.6 percent ($N=9$, range 7.1–23.3 percent), respectively. Derived protein values compare favorably with those reported by other authors. Herndon and Hove (1955) reported 41.9 percent protein for soft pellets and 14.8 percent protein for hard pellets in experimental California-white rabbits (*Oryctolagus cuniculus*). Griffiths and Davies (1963) estimated soft feces of rabbits contained 24.4 percent protein, 81 percent of which was in the form of bacterial cells. They reported bacterial cells composed 56 percent of the dry weight of soft feces. Other comparative estimates of protein content in the soft feces of domestic rabbits were 37.8 percent (Huang et al. 1954) and 28.5 percent

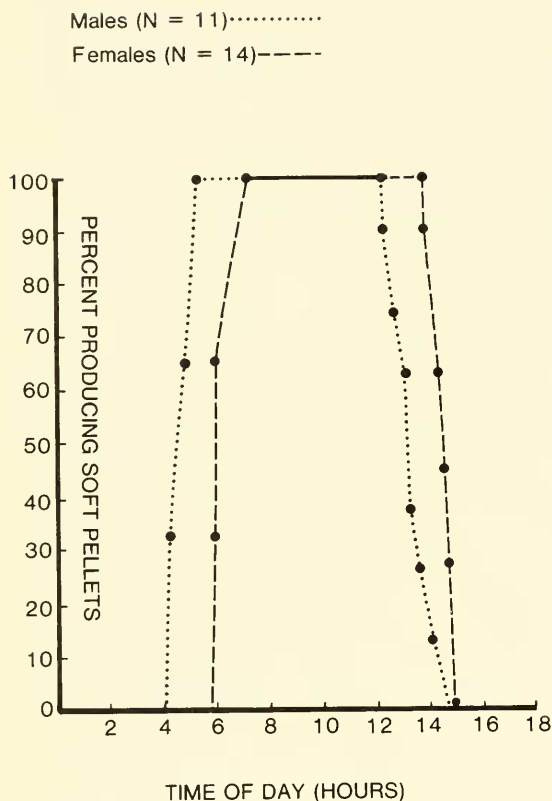


Fig. 3. Percent of male and female black-tailed jackrabbits producing soft pellets at the taenia coli muscle in the large intestine.

for soft feces and 9.2 percent for hard feces (Kulwich et al. 1953). Thacker and Brandt (1955) reported 37.4 ± 3.2 percent protein for soft feces and 18.7 ± 1.7 percent protein for hard feces in the Dutch rabbit.

Pellet Transition Periods

When a transition zone was found in the rectum of a black-tail, the degree of distinctness between the two types of pellets was noted. In our samples, 17 of 19 transition zones were very well defined and distinct, often with immediately adjacent pellets of the two types. In the other two cases, the transition zone included up to 10 cm of semihard pellets separating the hard and soft pellet types. Distinct transition zones were found for both early morning and afternoon periods of pellet transition.

Male black-tailed jackrabbits had initiated the transition from hard to soft pellets as

early as 0414 hours (Fig. 3). The transition period for both sexes ranged from 0414 to approximate completion by 0715 hours. Males sampled were complete in the initiation of their transition by 0500 hours, whereas females sampled were not all complete by 0700 hours (Fig. 3). All black-tails had made the transition to the production of soft pellets by 0730 hours. Soft pellets made up the entire composition of the rectum in all black-tails by 0915 hours.

Several male black-tails began the transition from soft to hard pellets as early as 1201 hours, or slightly before (Fig. 3). Female black-tails tended to initiate the same transition later in the afternoon. The earliest noted transition for a female was 1335 hours and most females initiated the transition between 1400 to 1430 hours. Most males had completed the transition to hard pellets by 1330 hours, but one male had started as late as 1450 hours (Fig. 3). Two females had not initiated the early afternoon transition by 1500 hours. Feces in the rectum of two males were composed entirely of hard pellets as early as 1408 hours and 1414 hours, respectively. No females had fully replaced the soft pellets in the rectum with hard pellets by 1500 hours.

The findings presented here generally support those reported by other authors (Spencer 1955, Watson and Taylor 1955, Lechleitner 1957, Hansen and Flinders 1969). Spencer (1955) found half the animals killed from 0900 hours to 1700 hours had soft pellets in their stomachs. There was evidence of soft pellets in stomachs of 21 of 25 animals killed at 1300 hours (Spencer 1955). Soft pellets were produced in all black-tailed jackrabbits collected from 0800 hours to 1000 hours in California, with evidence of the hares starting to reingest them (Lechleitner 1957). Amorphous pellets of the European hare (*Lepus europaeus*) were found in the recta of hares killed between 0600 hours and 1600 hours; all animals killed between 0800 hours and 1200 hours contained soft pellets in their recta (Watson and Taylor 1955). Lechleitner (1957) reported soft feces being produced and swallowed during the daylight hours, starting at 0600 hours and being replaced by hard feces by 2000 hours. However, the exact time of death was not known for the black-tails used in the sample, and

sample sizes were minimal during the early morning hours. With the knowledge of the exact time of death, the periods of transition in pellet types in the black-tailed jackrabbit were more precise in our study. Lechleitner (1957), in reporting the cycle of reingestion and production of soft pellets in the black-tailed jackrabbit in California, found the period of occurrence of soft pellets in the rectum may extend to as late as 2000 hours. Our findings do not support his conclusion. We suggest that, although pellets may be found in the rectum as late as 1600 hours or 1700 hours, the transition to hard pellets in the afternoon is essentially completed by 1330 hours for males and 1430 hours for female black-tails. Our data support the theory that males begin the transition from hard to soft pellets earlier in the morning than do females. This relationship was significant ($P < 0.05$) using the Mann-Whitney-Wilcoxon 2-independent sample procedure. Females initiated the transition from soft to hard feces significantly later ($P < 0.01$) in the afternoon than males. Lechleitner (1957) found no evidence that indicated any seasonal trend of reingestion in the black-tailed jackrabbit. Thus, this relationship may in fact be a year-long phenomenon.

The stimulus-response mechanisms causing the apparent dimorphism in behavioral physiology between the sexes is not known. However, reasons why this occurs may include partitioning of temporal feeding activities to reduce intersexual competition. This may be especially critical near the end of the winter season when forage above the snow level may be limiting, and when females are in late gestation or lactating. Intraspecific competition is maximal under peaking population cycles as well as during climatic seasons of stress. Intersexual segregation of temporal feeding cycles may tend to reduce this competition. Because of the higher energy requirements of gestation and lactation, female black-tails may feed later into the morning hours than males. Lactating females may suckle leverets in the early morning hours, and this demanding activity may help delay the production of soft pellets. In addition, females may reingest soft pellets later into the afternoon than males, thereby maximizing feeding efficiency and digestability of ingested forage.

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